How to Explain the Short Face of the New World Monkey

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INTRODUCTION

In many mammalian lineages, larger animals tend to have relatively longer faces and smaller brain cases. For instance, RADINSKY (1984) shows that both in equid phylogenetic sample and recent carnivoran sample many facial measurements scale to brain case length by scaling factors of approximately 1.3. This mammalian general tendency of positive allometry of facial skeleton on brain case can be intuitively recognized also in primate lineages. In fact, large animals in several primate higher taxonomic groups show disproportionally long faces; e.g. *Megaladapis* in lemuroid (SIMONS, 1972; MACPHEE, 1987), *Papio* in cerecopithecoid, *Gorilia* in hominoid etc. However, New World monkeys have been characterized uncritically by their short or hafted faces irrespective of their body size variation (LE GROS CLARK, 1959; SIMONS, 1972; ROSENBERGER, 1977). The author also suggested, in a previous issue of this series (MOURI, 1988), near isometry of facial skeletons to brain cases among ordinary ceboids, that is recent ceboids excluding *Alouatta* and *Saimiri*.

In this paper, actual cranio-facial relationships among ceboid monkeys are numerically estimated by allometric analyses (GOULD, 1975) and a hypothesis explaining the resulting relationship will be presented. Nasion-inion length (*NI*) and basion-prosthion length (*BP*) are used, respectively, to represent dimensions of brain case and facial skeleton. Nasion-inion length is the maximum length of brain case measured from nasion. Basion-prosthion length is measured linearly from basion to prosthion. Regression analysis is used to estimate the straight line of best fit. Though there are some claims against the use of regression analysis (KERMACK and BALDANE, 1950; NARVEY and MACE, 1982; MARTIN, 1981), there will be no serious problem in this analysis since the correlation coefficients between the two variables compared are in main cases high enough as will be apparent in the following.

LINEAR REGRESSION ANALYSIS OF RAW DATA

Regression line of *BP* (facial length) on *NI* (brain case or cranial length) is calculated by least square method. Using 14 points representing 14 genera of New World monkeys (Table 1, see details in MOURI, 1988), the regression equation is

$$BP = 1.188NI - 16.093 \quad r = 0.914 \ (N = 14).$$

If long faced *Alouatta* and long skulled *Saimiri* are excluded from the analysis, the regression equation is

$$BP = 1.035NI - 8.299 \quad r = 0.989 \ (N = 12).$$

Table 1. Brain case (nasion-inion) lengths (NI) and facial (basion-prosthion) lengths (BP) in 14 ceboid genera

Genus	N	NI	BP
Cebuella	3	30.3	24.0
Leontopithecus	9	46.6	39.1
Callimico	1	42	34
Saimiri	15	53.7	38.4
Cebus	17	75.4	68.2
Callicebus	12	48.9	43.6
Aotus	7	50.3	42.7
Pithecia	3	59.7	57.0
Chiropotes	10	66.1	59.4
Cacajao	9	71.6	63.9
Lagothrix	9	82.8	78.9
Ateles	5	85.6	74.8
Brachyteles	9	87.4	88.0
Alouatta	25	79.5	108.0

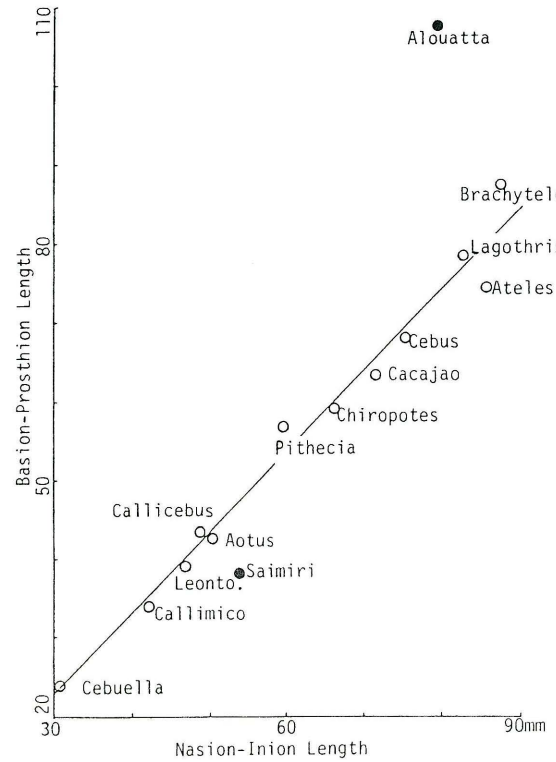

Fig. 1. Linear regression curve of facial (basion-prosthion) length on brain case (nasion-inion) length calculated by using 12 points of ordinary ceboid genera (open circles). Points for *Alouatta* and *Saimiri* (closed circles) are not used for the calculation.

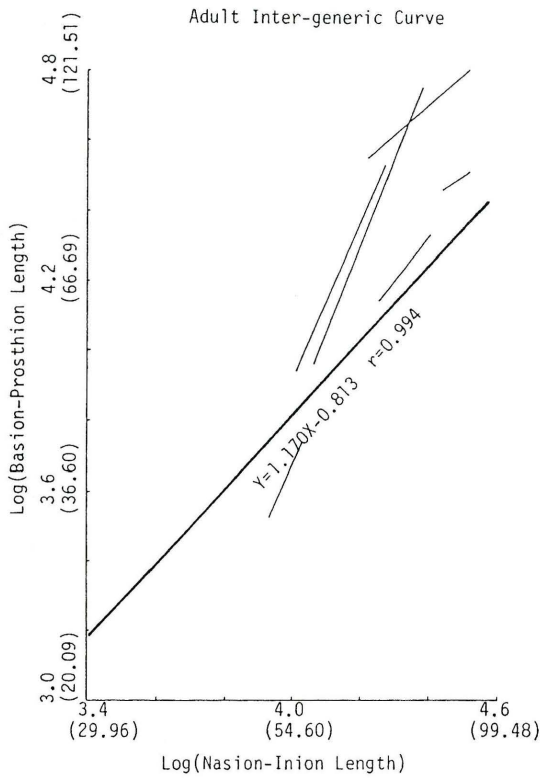

Fig. 2. Adult inter-generic allometric curve (heavy line) obtained by linear regression analysis of log transformed facial length on log transformed brain case length, using 12 ordinary ceboid genera as in Fig. 1. For thin lines, see legends of Figs. 3 and 4.

The regression coefficient and the correlation coefficient approaches very near to unity, respectively, from 1.188 to 1.035 and from 0.914 to 0.989. The absolute value of positional constant is reduced markedly from 16.093 to 8.299. As shown in Fig. 1, deviations of the points representing ordinary ceboid genera from the regression line are small. If the positional term or y-intercept could be interpreted to be zero or negligible, the equation would automatically mean isometry of facial length on cranial length and there would be no need to further apply logarithmically transformed linear regression analysis or allometric analysis. But, considering the small size of callitrichids, the positional constant of −8.299 can not be neglected.

LOG TRANSFORMED LINEAR REGRESSION ANALYSIS (ALLOMETRIC ANALYSIS)

Regression line of log transformed *BP (Y)* on log transformed *NI (X)* is calculated. Natural logarithm is used. Using 14 points, the equation is

$$Y = 1.269X - 1.206 \quad r = 0.958 \quad (N = 14).$$

Using 12 points of ordinary ceboid genera, the regression equation is

$$Y = 1.170X - 0.813 \quad r = 0.994 \quad (N = 12).$$

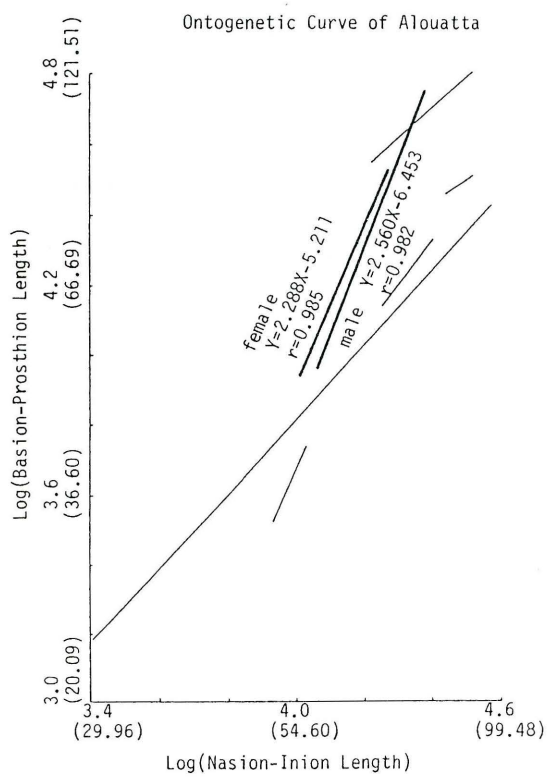

Fig. 3. Male and female ontogenetic cranio-facial allometric curves of *Alouatta seniculus* (heavy lines). For thin lines, see legends of Figs. 2 and 4.

Excluding two points representing *Alouatta* and *Saimiri,* the regression coefficient (the allometric exponent) approaches to that of isometric relationship of unity, from 1.269 to 1.170 (Fig. 2). However, because of almost complete correlation between X and Y (0.994), the allometric exponent of 1.170 is significantly different from the isometric exponent of unity at 1% level of significance. The confidence interval of the allometric exponent of 1.170 at 99% level is from 1.300 to 1.040, 95% confidence interval being from 1.261 to 1.079 (SNEDECOR and COCHRAN, 1967). Before attempting to explain the above equation representing adult interspecific allometry of ordinary ceboids, results of some other types of allometric analyses (GOULD, 1975) are presented briefly.

Figure 3 shows cross-sectional ontogenetic allometric curves of male and female samples of *Alouatta seniculus* (see details in MOURI, 1984). The regression equation of male sample is

$$Y = 2.560X - 6.453 \quad r = 0.982 \quad (N = 5).$$

The equation of female sample is

$$Y = 2.283X - 5.211 \quad r = 0.985 \quad (N = 4).$$

Sampled range of ontogeny or growth is from the completion of deciduous dentition to the adulthood both for male and female samples. The ontogenetic curves (Fig. 3) illustrate the earlier development of brain case than that of facial skeleton and faster growth rate of facial skeleton

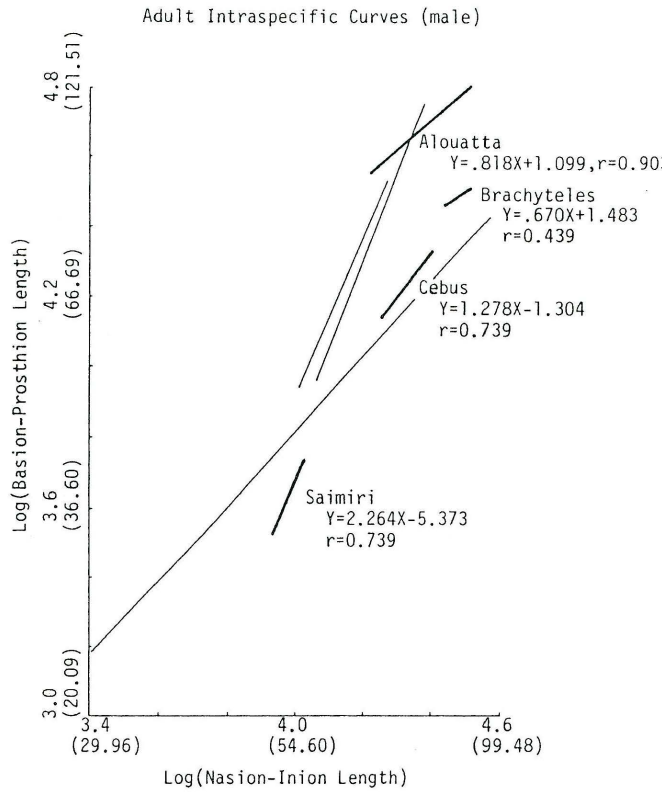

Fig. 4. Adult male intraspecific cranio-facial allometric curves of *Alouatta seniculus*, *Brachyteles arachoides*, *Cebus apella*, and *Saimiri siureus* (heavy lines). For thin lines, see legends of Figs. 2 and 3.

than that of brain case after the completion of deciduous dentition. Though the youngest animals of *Alouatta seniculus* studied have the crania-facial proportions not far from adult animals of ordinary ceboids, the similarity itself should be considered as a uniqueness of *Alouatta* because young animals of other ceboid genera have relatively much shorter faces than adult animals of the same species.

Male adult intraspecific allometric curves of *Alouatta seniculus*, *Brachyteles arachnoides*, *Cebus apella* and *Saimiri sciureus* are shown in Fig. 4. The log transformed regression equation of *Alouatta* is

$$Y = 0.918X+1.099 \quad r = 0.903 \quad (N = 25).$$

The equation of *Brachyteles is*

$$Y = 0.670X+1.483 \quad r = 0.439 \quad (N = 9).$$

The equation of *Cebus* is

$$Y = 1.278X-1.304 \quad r = 0.739 \quad (N = 17).$$

The equation of *Saimiri* is

$$Y = 2.264X-5.373 \quad r = 0.739 \quad (N = 15).$$

In *Alouatta* and *Brachyteles*, the allometric exponents of facial length on brain case length are less than unity, and in *Cebus* and *Saimiri* the exponents much surpass unity. This suggests higher

variabilities of facial length in adults of cebids and lower variabilities of it in adult atelids of ROSENBERGER (1979a, 1981). If this tendency is confirmed, it is very interesting because it apparently contradicts our intuitive expectation. But in these equations representing adult intraspecific allometries low values of correlation coefficients make the criticism against the use of regression analysis (HARVEY and MACE, 1982) pertinent, especially for the interpretation of that of *Brachyteles*. Too overt interpretations should not be emitted here. Larger and wider samples are needed.

HPYPOTHESIS EXPLAINING THE LOW ALLOMETRIC EXPONENT IN CEBOIDS

Regression analysis of logarithmically transformed facial length on logarithmically transformed brain case length among ordinary ceboids produces the regression coefficient of 1.170. This means that facial length scales to 1.170 power of brain case length in ordinary ceboids. The allometric exponent of 1.170 is not far from one or the isometric exponent, but significantly different from one at 1% level. Here, it is attempted to explain the allometric exponent of 1.170, constructing an allometric equation the allometric exponent of which is at least in the range of 5% confidence interval of 1.170 (from 1.261 to 1.079). In the following, the allometric coefficients of allometric power functions, which are equivalent to the y-intercepts of log transformed regression equations, will be omitted from the equations for the sake of simplicity. Therefore, a sigh of equality (an equal mark) should be read as designating proportional equality.

Assuming geometric similarity among ordinary ceboid faces

$$\text{Log (Facial length)} = 1/3\times \text{Log (Facial volume)} \quad (1).$$

Further, assuming isometric relationship between facial volume and metabolic rate in ordinary ceboids, the equation (1) will be

$$\text{Log (Facial length)} = 1/3\times \text{Log (Metabolic rate)} \quad (2).$$

It is well known that metabolic rate of mammals scales to 3/4 power of body mass (KLEIBER, 1932; SCHMIDT-NIELSEN, 1984). Then, the equation (2) will be

$$\begin{aligned}\text{Log (Facial length)} &= 1/3\times 3/4\times \text{Log (Body mass)}\\ &= 1/4\times \text{Log (Body mass)} \quad (3).\end{aligned}$$

The use of allometric equations is said to be originated by SNELL in 1891 to express biological relationship between brain mass and body mass in mammals (SCHMIDT-NIELSEN, 1984; MARTIN, 1981; GOULD, 1975). It is widely accepted that brain mass is proportional to body surface area, that is, Log (Brain mass) = 2/3×Log (Body mass), though there are some criticisms (e.g. MARTIN, 1981). If the term of body mass in the equation (3) is substituted by that of brain mass of this equation, the equation (3) will be

$$\begin{aligned}\text{Log (Facial length)} &= 1/4\times 3/2\times \text{Log (Brain mass)}\\ &= 3/8\times \text{Log (Brain mass)} \quad (4)\end{aligned}$$

And, assuming geometric similarity of brain case

$$\begin{aligned}\text{Log (Facial length)} &= 3/8\times 3\times \text{Log (Brain case length)}\\ &= 9/8\times \text{Log (Brain case length)}\\ &= 1.125\ \text{Log (Brain case length)} \quad (5)\end{aligned}$$

The allometric exponent of the equation (5) of 1.125 is very near to the actually obtained value of 1.170 and well within the 5% confidence interval of it (from 1.079 to 1.261). In deriving the equation (5), five assumptions are made, three of which have no confirmation or reputation at

least presently to my knowledge; namely, geometric similarity of face, isometry between facial volume and metabolic rate, and geometric similarity of brain case. The suppositions of geometric similarities of face and brain case among ordinary ceboids are apparently incorrect or at least inaccurate since we can distinguish facial or brain case shapes of two different genera of ceboids by unscaled photographs or illustrations in most cases. But these two assumptions, being *a priori* ones at the very beginning of this paper when I selected facial and brain case lengths to represent facial and brain case dimensions, should be accepted here whether willingly or reluctantly.

As to the validity of the other assumption of isometry between facial volume and metabolic rate, the similarity of the two equations (the observed equation among ordinary ceboids and the equation derived from the assumption) and the strong correlation accompanying the observed equation tentatively urge us to believe in it. However, it is hardly possible to expect a simple chemical or mechanical solution of the the assumption, considering highly composite nature of the mammalian face consisting of various physiologically important organs, which in turn seem to have various values of allometric exponents to body size. For example, volume of air tract in the facial region or nasal cavity seems isometric to body mass, considering both lung volume and tracheal dead space isometries to body mass (SCHMIDT-NIELSEN, 1984; TENNEY and BARTLETT, 1967). Scaling of primate cheek tooth size against body weight shows isometry or slightly negative allometry (GINGERICH and SMITH, 1985). All of the masticatory muscles examined by CACHEL (1984) are isometric to adult body size among anthropoid primates. On the other hand, special sense organs generally show strong negative allometries to body size; e.g. eyeball volume to body weight and orbital diameter to skull length from prosthion to inion (CARTMILL, 1970, 1980; SCHULTZ, 1940; KAY and CARTMILL, 1977). Moreover, there are perhaps some compensating or regulator spaces in a face, such as paranasal pneumatizations (HERSHKOVITZ, 1977). But, almost all allometric analyses entail this kind of problem; the difficulty of reducing an overall dimension to its anatomical components and synthesizing an overall parameter from various parameters of components. On the contrary, this difficulty is a necessary by-product of the major advantage of allometric method to extract overall bivariate relationships among biological entities.

GENERAL DISCUSSION

In the preceding section, the slope of 1.170 of the interspecific (or intergeneric) allometric equation among ordinary ceboids is tentatively explained by assuming isometry between facial volume and metabolic rate. Here, the strong linearity or the high degree of correlation between facial length and brain case length among ordinary ceboids will be discussed.

In most allometric analyses, especially in those concerning interspecific comparisons, linearity between the two variables compared is generally interpreted to mean underlying physical, chemical, physiological or phyletic constraints or laws (MCMAHON, 1973; GOULD, 1975; SCHMIDT-NIELSEN, 1984; MARTIN, 1981). In this study, the linearity of craniofacial relationship among ordinary ceboids is shown to be very strong. But the strong linearity can not be interpreted to be caused by a general and rigid constraint by physical or chemical law, because the strong linearity is attained by excluding outliers; i.e. *Alouatta* and *Saimiri*. And, considering the proposed long independent histories for some ceboid genera; e.g. *Aotus*, (SETOGUCHI and ROSENBERGER, 1987) and *Saimiri* (ROSENBERGER, 1979b), the exclusive use of phyletic constraint or phylogenetic inertia for the explanation seems also unattractive since a phyletic inertia enduring more than twen-

Table 2. Deviations of facial lengths of 14 ceboid genera from the linear regression (LR) and allometric (AL) curves

Genus	LR	AL
Cebuella	0.0	0.9
Leontopithecus	–0.6	–0.8
Callimico	–1.2	–1.2
Saimiri	–8.5	–8.9
Cebus	–1.5	–1.5
Callicebus	1.6	1.3
Aotus	–0.7	–1.1
Pithecia	3.9	3.5
Chiropotes	–0.4	–0.7
Cacajao	–1.7	–1.9
Lagothrix	1.1	1.5
Ateles	–6.1	–5.5
Brachyteles	5.1	5.6
Alouatta	33.8	34.0

ty million years resembles something like a Platonic idea though the principle of parsimony logically demands phyletic conservatism. Though I can not identify it at present, a more proximate cause seems much more reasonable, such as head balance on the atlas (SCHULTZ, 1955; MATSUMOTO, 1983) or mere sampling error. BOUVIER (1986) offers some opposing evidence to relying on sampling error, who shows higher degree of correlation between body mass and mandibular length among New World monkeys than among Old World monkeys. In anthropoid primates, mandibular length is roughly equal to and slightly shorter than facial length. Using the words of GOULD (1975) after trying to identify causes of 0.66 scaling of mammalian brain-body relationships, it remains an "unresolved mystery".

It is in some cases easier to attack deviations from the line than to attack directly the linearity of the line itself, for in a sense a rule is a rule because it can not be easily explained by or reduced to more general principle(s). Table 2 lists the deviations of facial lengths of individual genera from those estimated by linear regression and allometric curves. Though the appearances (and underlying methodologies) of the two equations are quite different and the correlation coefficients accompanying them indicate slight difference, the two sets of deviations are in effect identical with each other. Therefore, only the deviations from the allometric curve will be discussed. The two genera, *Alouatta* and *Saimiri,* which are excluded from the analysis, have by far the largest deviations. The deviation of *Alouatta* is 34.0 mm and that of *Saimiri* is –8.9 mm. The directions of the deviations might be interpreted as an indication of the relative facility of the directions taken by new adaptations or reorganizations. The craniofacial reorganization of *Alouatta,* which can be said a peramorphosis in the heterochronic terminology (GOULD, 1977), is usually explained by the basicranial and facial elongation resulting from vocal specialization (BIEGERT, 1963; WATANABE, 1982), while there is also a prediction "out on a limb" that *Alouatt* is a phyletic giant which has relatively small brain as *Gorilla* (GOULD, 1975). On the other hand, *Saimiri* is well known to have a relatively large brain, an exceptional elongation of the occipital region of the skull (LE GROS CLARK, 1959; ROSENBERGER, 1979a) and a uniquely anterior position of the occipital condyles (SCHULTZ, 1955; MATSUMOTO, 1983), though the adaptive significances of these characters are not clear. These characters of *Saimiri* suggest a phyletic dwarfism brought about by a kind of heterochronic events as in talapoin evolution (GOULD,

1975); i.e. progenesis, postdisplacement or neoteny (MCKINNEY, 1988). Since the proposed lineage of *Saimiri* from *Dolicocebus* of late Oligocene via *Neosaimiri* of middle Miocene (ROSENBERGER, 1979b) has witnessed no marked size change, the phyletic dwarfism should have occurred very old if it had.

Deviations of other genera are not marked. Only *Brachyteles* (5.6 mm), *Ateles* (–5.5 mm), and *Pithecia* (3.5 mm) have the deviations the absolute values of which exceed 2 mm. These minor deviations of ordinary ceboid genera can not be successfully correlated with such factors as food habit (CACHEL, 1979; KAY, 1975), level of intermale competition which correlates with canine dimorphism (RAY et al., 1988), locomotion (NAPIER and NAPIER, 1967) or phylogenetic taxonomies (ROSENBERGER, 1979a; FORD, 1986).

SUMMARY

In ordinary ceboid genera excluding *Alouatta* and *Saimiri*, the facial length is shown to scale to 1.170 power of the brain case length by allometric analysis. Exceptionally strong correlation (r = 0.994) is found between these two variables. The allometric exponent of 1.170, which is statistically different from one at 1% significance level, is explained by assuming an isometry between facial volume and metabolic rate among ordinary ceboid genera. The difficulty is ascertained to explain the high degree of linearity witnessed by the correlation coefficient of 0.994.

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